The thylacine's last straw: epidemic disease in a recent mammalian extinction

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ABSTRACT

While anecdotal accounts exist in the literature of epidemic disease as a significant factor in recent mammalian extinctions, harder data has not previously been presented. The statistics from the deliberate killing of thylacines as a pest species support contemporary records at the turn of the twentieth century, of an epidemic disease in thylacines and other marsupi-carnivores. For the first time, detailed symptoms and statistics of the disease are presented, as recorded by museum staff, and zoological-garden curators and veterinarians. It is argued that the effects of the disease in captivity, which more than halved thylacine longevity, and preferentially affected juveniles, are conformable with the expression of the disease recorded amongst wild thylacines, and demand a recognition of the importance of this disease as a major factor in the thylacine's recent extinction, and its consideration as an influential factor on the distribution and population dynamics of extant marsupi-carnivores. It also practically demonstrates the obvious potential for disease to have been involved in megafaunal extinctions in the past.

Key words: Thylacine, Tasmanian devil, marsupi-carnivores, extinction, disease, megafauna.

Introduction

The suggestion that a hyperdisease, introduced by humans or their commensals invading a geographic entity for the first time, may have been a significant factor in late-Pleistocene mammalian megafaunal extinctions (MacPhee & Marx, 1997), warrants a careful re-examination of the evidence for the involvement of disease in any recent mammalian extinction. Introduced disease organisms appear to have been significant factors in the extinction of some gastropod (Cunningham & Daszak, 1998) and amphibian (Pounds *et al.* 2006) species, and in some recent avian extinctions in Hawaii and New Zealand (Groombridge, 1992; van Riper *et al.* 1986, Warner, 1968). This avian data has led discussion, debate and modelling of the possibility of hyperdisease amongst late-Pleistocene mammalian faunal assemblages (Lyons *et al.* 2004). While recent mammalian loss has occasionally been accompanied by anecdotal accounts of disease - comment re distressed and diseased individuals accompanies the extinction early last century of two endemic murids on Christmas Island (Andrews, 1909; Pickering & Norris, 1996) - harder data has not previously been offered for a disease-associated, recent mammalian extinction.

The thylacine (marsupial wolf, or Tasmanian tiger, *Thylacinus cynocephalus*) lived in stable monogamous pairs, presiding over a wide-spread hunting territory. Slow breeding and long-lived (nineteenth-century records suggest over 14 years in captivity[1]), they produced up to four young every second year. Adolescent thylacines, having spent 12 to 18 months co-operatively pack hunting with their parents, finally left the family group before the next generation of young became semi-independent of the pouch. Adolescent thylacines potentially travelled widely to establish a pair bond and their own hunting territory (not necessarily in that order); such behaviour allowing for a frequency dependant transmission of any epidemic disease, with even greater adolescent dispersal required after the appearance of the disease within the species. After the invasion of Tasmania by European colonists at the commencement of the nineteenth century, thylacines began to suffer prolonged predation; labelled as a pest and killed both by farmers (over the rural myth of the thylacine as a significant sheep-killer [Paddle, 2000]), and by snarers for the fur trade (over the annoying, but understandable, tendency for any marsupi-carnivore to view a snared possum, wallaby or kangaroo as a free-lunch).

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[1] In April 1856, unannounced and unexpected, a "Mr. Martin" arrived in London at Regent's Park Zoo with a male thylacine. It shares the record for the longest-lived captive thylacine; as London specimen ***iii***, later on-sold to become Berlin specimen ***i***, it survived for 103 months in European captivity (and this is the longevity figure given for the specimen in Table 5). Its April arrival, however, necessarily followed a two to three month ocean voyage, indicating that it left Tasmania in January or February 1856. The fact that it survived the journey also suggests that it was well-adapted to captivity before departure. While that is all that is definitely known of the origins of this specimen, there is a conformable history of a captive thylacine to pair with it. Ronald Campbell Gunn, living near Launceston, took a thylacine into captivity in June 1851 (which must, at a minimum, given the specimen's survival, have been the product of a late winter breeding the previous year, and thus born around September 1850). In October 1853 he placed it under the care of Chester Wilmot who initially took the thylacine to Hobart, intending for it to accompany him on his return voyage to England. Henry Propsting, however, who had opened the first zoological garden (and museum) in Hobart, became aware of the thylacine's presence, and wrote to Gunn, pulling out the nationalistic stops and requesting the opportunity to display the thylacine locally, rather than having it sent abroad. To this Gunn agreed, and the thylacine entered the display at Propsting's zoo in January 1854, with the extracted promise, however, that Propsting would forward the specimen to London if or when he had no further use for it. Propsting closed his zoo, left Hobart and retired to his country estate in January 1856. Having decided in 1855 to close the zoo, he offered his museum collection (largely based on departed specimens from the zoo) to the Royal Society of Van Diemen's Land. Many of Propsting's museum specimens were greatly received by the Society, but there was no thylacine material in the Propsting museum collection, suggesting that the animal was still alive. In accordance with the agreement he made with Gunn, Propsting would have placed the thylacine on board ship, bound for the Zoological Society of London, around January 1856. While no archival records have as yet been found that directly link this January 1856 Hobart departure and April 1856 London arrival, circumstantial evidence points to these being one and the same specimen, and suggests that, on its death in Berlin, this thylacine was at least 14 years and two months of age. As a further point, it also needs to be recognized that nineteenth-century, captive-marsupial longevity did not reach the levels obtained later in zoological gardens in the twentieth and twenty-first centuries, as experience, husbandry and veterinary knowledge of marsupials has improved over time (Holz, 2008).

Casually collected anecdotal records and early bounty analyses have, at times, prompted the suggestion that disease was a major factor in the extinction of the species, that occurred when the last known specimen (*xxix*) died in Hobart Zoo during the night of 7th September, 1936.[2] Representative examples of authors claiming a disease-assisted extinction include Hickman (1955), Guiler (1961), Sharland (1971a), MacPhee and Marx (1997) and Paddle (2000). However, the scattered and largely anecdotal evidence previously available allows of alternative explanation, and, on not unreasonable grounds, these claims have been previously dismissed as wanting (Johnson, 2006). This paper provides the first detailed description by professional scientists of the epidemic disease in the thylacine. Data is presented on captive longevity that directly relates to the bounty records and strongly suggests that the disease was a significant factor leading to the extinction of the species.

Initial Disease Recognition

The first professional scientists to recognise that something dramatic had occurred to the thylacine in north-eastern Tasmania at the end of the nineteenth century were Wm. McGowan, Superintendent of the Launceston City Park Zoo, and Herbert Scott, Director of the Queen Victoria Museum, Launceston.

In the eight years from the first display of the species in June 1885, to July 1893, Launceston Zoo obtained 21 thylacines, largely from north-eastern Tasmania. (Two juveniles, one obtained from Montagu in the north-west of the state in November 1885 [*iii*], the other from Bream Creek in the south-east in June 1886 [*v*] being the only known exceptions.) However, in the next eight year period, up to June 1901, McGowan managed to obtain only six thylacine specimens. (For the first five years, between July 1893 and June 1898, McGowan was unable to obtain any thylacines, from any locality whatsoever, for the zoo. The six specimens referred to all arrived in the last three years of this eight-year time period, from June 1898 to June 1901, starting with three specimens [*xxii* to *xxiv*], not from the north-east, but from the Western Tiers, obtained in June and December 1898 and July 1889.) McGowan wrote to Melbourne Zoo in November 1906 that "Tasmanian Wolves were almost extinct & Tasmanian Devils [*Sarcophilus harrisii*] very difficult to obtain" (letter November 1906). In writing to the National Museum of Victoria, McGowan noted that "complete skeletons" from thylacines possessing "damaged or rotten skins" were available, but that fine, entire specimens of the species were now almost impossible to find (letter 21/6/1909).

Scott commented upon the recent difficulty of obtaining thylacine specimens for the museum from trappers, offering 7/6 for the body of a thylacine, more than doubling the price to 17/6 if the skin was in a fit state for preservation (letter 10/5/1899) – such adult skins, no matter the quality, having already raised for the trapper at least £1 from the government bounty. He apologized to his professional colleagues for the necessity of now sending less-than-perfect specimens to other museums as representatives of the species - "I think it worth sending a damaged animal … [as] good specimens are rare and not easy to obtain" - and noting that the most recent thylacine dying in Launceston Zoo was "in poor condition and fit for nothing" (letter 3/8/1901). Externally, such "poor condition" specimens exhibited areas of significant hair loss, skin lesions and mange. The National Museum of Victoria, anxious for any additional thylacine specimens, was prepared to take such "poor condition" specimens off the hands of the Queen Victoria Museum, and were pleased to note how "by exercising care, we have been able to save the skin, which showed traces of mange" (Kershaw, letter 4/6/1903).[3]

Scott was also aware that the disease was not just restricted to thylacines, but that it had also dramatically reduced Tasmanian devil numbers (letter 25/4/1904), to the point where he was also forced to send damaged, less-than-perfect devil specimens to other museums (letter 20/6/1904). McGowan similarly recognised the problem that the skins of diseased devils that died in the zoo presented, in the setting-up of full mounts, "because sometimes pieces of fur get knocked off" (letter 18/6/1907). As recalled by the farmer Lewis Stevenson (interview 1/12/1972): "devils … got the mange like the tigers … their hair fell out and left the black skins bare in the bad ones".

Few professional scientists at the time published comment on the existence of an epidemic disease affecting marsupi-carnivores, but recognition of the existence of the disease is to be found in the letters passing between them, in their daily institutional records, and in their private diaries; such being the primary sources on which this paper is based. Note, however, that Albert Le Souëf jnr, with a background knowledge of marsupi-carnivore arrivals at Melbourne Zoo, and Moore Park and Taronga Zoos, Sydney; Harry Burrell, the widely travelled naturalist and mammalogist; Frederic Wood Jones, Professor of Anatomy at the University of Adelaide; and Ellis Troughton, Curator of Mammals at the Australian Museum, Sydney, did publish comment as to the existence of an epidemic disease on the mainland amongst the Dasyurid marsupi-carnivores at the turn of the twentieth century (A.S. Le Souëf & Burrell, 1926, p324; Troughton, 1941, p43; and Wood Jones, 1923, p92).

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[2] Throughout this paper, individual zoological garden thylacines are identified by roman numeral alone, in both text and tables 5 and 6, indicative of the chronological order of their display. Individual Tasmanian devils mentioned in the text are identified by roman numerals preceded by "S". These designations represent a work-in-progress, with some recently discovered specimens, falling between two previously identified individuals, temporarily identified with the roman numeral of the earlier specimen, followed by the letter "a".

[3] Unfortunately, none of these mangy skins currently remain in the Museum's collection, as later curators and collection managers had them destroyed, on the assumption that these damaged skins were exhibiting contemporary Dermestid and/or moth attack.

Two commonly reported labels for the disease were recalled by farmers, trappers and old-timers. Explaining some of the immediate internal effects of fever (lassitude, coughing, diarrhoea and thinness), and vulgarly presented as the likely origin of the disease, is its description as "distemper". (For anecdotal reference thereto see Cotton [interview 1980], Guiler [1958, 1985], Hickman [1955], Sharland [1956, 1971a, letter 23/6/1972] and Skemp [1958].) Describing the longer-term, external effects of the infection (lesioned skin with significant hair loss and external bleeding), is its description as "mange". (For anecdotal reference to mange see Brown [1972, 1973], Guiler [1986], Sharland [1956, 1960, 1971a, 1971b, letter 23/6/1972] and Stevenson [interview 1/12/1972].)

Alongside these contemporary written accounts by professionals, and the oral-history records of farmers and bushmen with their recollections of the disease, are data on thylacines killed, both from the Van Diemen's Land Company Woolnorth property in north-western Tasmania, and the Tasmanian-wide government bounty scheme (*Destruction of Native Tigers*) raised against the species.

The Background Extermination Rate

The data on killed and captured thylacines at the Woolnorth property of the Van Diemen's Land Company (Table 1 - based on Guiler, 1961, tables II and IV; and Guiler, 1985, tables 2.1 and 2.3; with minor corrections and additions relating to ten specimens from the present author's archival research) suggests a species in decline. Of the 161 thylacines known to have been killed or captured on Woolnorth during the 60 years from 1874 (the date of the earliest preserved station diary and account book) to 1933, a little under half of them, some 66 specimens, were killed in the first ten years. In a typical illustration of local species decline, in the second ten-year period, from 1884 - 1893, only 29 thylacines were killed. Such classic illustration of decline did not continue.

Significant behavioural change occurred in either the thylacine or human population at Woolnorth towards the end of the next ten-year period. In just two years, 1900 and 1901, 28 thylacines were destroyed on Woolnorth. In total, 55 thylacine specimens were killed during this third ten year period, from 1894 - 1903. During this time, no determinable behavioural changes have been recorded for the humans with particular thylacine interests on Woolnorth. There was only ever one "tiger man" employed at any one time at Woolnorth (and this was not, in any sense of the words, a full-time position [Paddle, 2000]), and no change was made to the level of bounty payment offered by the Van Diemen's Land Company; which simply matched that of the government bounty scheme, from which recompense was later recovered for the bounties paid by the Company. The behavioural change suggested would thus appear to be thylacine-based, with an increased ease of capture and killing, or the discovery of dead specimens, being a product of the disease. The destruction of these 55 thylacines represented the effective end of the species as a self-sustaining unit on the 150,000 acre (60,700 hectare) Woolnorth property (within which the majority holding of the land lay to the north of Mt. Cameron).

From 1904 onwards, occasional adolescent immigrants from the surrounding wilderness areas were snared as they passed through Woolnorth, or attempted to settle and breed, but they were few and far between. During the next ten years, 1904 - 1913, only seven thylacines were killed or captured (one in September 1906, and an entire settled family of two adults and four young in late May and early June 1909). For the ten years from 1914 – 1923 there were no thylacines killed or captured at Woolnorth. In the next decade, 1924 – 1933, four thylacines were captured alive on Woolnorth: a juvenile was snared in August 1924, an adult pair was captured in July 1925, and the last known thylacine definitely recorded from Woolnorth, an adult female, was captured in October 1925.

Table 1. Thylacines killed or captured alive at Woolnorth, 1874 – 1933.

Year	Killed or captured	Year	Killed or captured
1874	7	1894	4
1875	11	1895	6
1876	5	1896	3
1877	8	1897	4
1878	7	1898	2
1879	1	1899	3
1880	5	1900	19
1881	9	1901	9
1882	4	1902	3
1883	9	1903	2
1884		1904	
1885		1905	
1886	1	1906	1
1887	3	1907	
1888	3	1908	
1889	2	1909	6
1890	6		
1891	7	1924	1
1892	2	1925	3
1893	5		

The background extermination rate at Woolnorth, from 1874 to 1899, with consistently reducing numbers of thylacines killed, by itself was likely to lead to local extinction. Against this steady decline the sudden, increased ease of capture of thylacines at Woolnorth at the turn of the twentieth century is most likely due to the arrival in north-western Tasmania of the slow and debilitating epidemic disease as it spread westwards across northern Tasmania. An unidentified bushman, interviewed by Lindsay Crawford at Long Hill, near Railton, noted a progressive decline of thylacines in north-western Tasmania. Before they died off "Tigers were very common around Smithton, & later still, beyond the Arthur River" (Crawford, interview notes 21-22/11/1952). Harry Wainwright, one of the last "tiger men" employed at Woolnorth by the Van Diemen's Land Company, recalled that the disease appeared in north-western Tasmania around 1899, and was expressed first of all in thylacines living between the Arthur River and Marrawah - Mt. Cameron area, while thylacines living to the north of Mt. Cameron initially remained healthy (interview 1/10/1972). The manager of the Van Diemen's Land Company, A.H. McGaw, also referred to the sudden disappearance of thylacines at the turn of the century: "Up to within a few years ago there were a large number of tigers on the Woolnorth Estate" (letter 10/7/1908). Of related interest is the comment by the naturalist, the Rev. Henry Atkinson, who, when passing through Woolnorth in the early 1900s, noted the absence of Tasmanian devils and native cats around Mt. Cameron (Atkinson, 2001, p224).

A new analysis of the total number of thylacines annually approved for government bounty payment is presented in Table 2, based on a re-analysis of the Lands and Surveys Department Ledgers (first undertaken by Eric Guiler in the early 1960s, Guiler 1961); a careful sifting of the Lands and Surveys Department correspondence files, municipal archives, and preserved archival records for the duration of the bounty from 22 Tasmanian police stations (Paddle, 2007). (This research is on-going – further police station archives for the 21 years of the bounty remain to be read by the author – thus the data presented in Table 2, whilst an improvement on previously published bounty analyses, is not to be taken as definitive.)

State-wide, the bounty shows a similar elevation in the total numbers killed for the years 1899 to 1902 to that recorded at Woolnorth, reflecting the arrival of the disease in the less-settled north-west. (Note, however, that the spread of the disease in southern Tasmania has not yet been accurately determined.)

Police station records of the bounty from north-eastern Tasmania reflect the difficulty Wm McGowan began experiencing after July 1893 in obtaining thylacine specimens from the north-east for Launceston City Park Zoo. (In fact, McGowan had to await the arrival of the new century before live thylacines were again obtained for the zoo from north-eastern Tasmania.) For example, in the five years, from 1891 to 1895, eight adult thylacines were presented to, and approved for bounty payment by, constables at the St. Helens' Police Station (St. Helens Police Station, 1907). No thylacines were presented for bounty payment in the first nine months of 1896. But then, for a brief period commencing in October 1896, five adult thylacines were presented for bounty payment in just six months; such increase reflecting a contemporary ease of obtaining distressed, diseased or dead thylacines encountered in the bush. But that was it. No further thylacines from the surrounding Portland District were presented for bounty payment to the police station during the remaining twelve years of the bounty's operation. Contemporary newspaper comment also recognized, and welcomed, this newfound scarcity of thylacines in north-eastern Tasmania: "Formerly tigers were very troublesome … on the North Esk River" (*Launceston Examiner,* 22/3/1899).

Prior to the spread of the disease, it was extremely unusual to find thylacines dead in a snare, and prospective bounty claimants were officially warned by the Tasmanian Lands and Surveys Department of this potential danger: "Tigers do not choke themselves with the snares, - it is a very rare thing to find one dead" (Braddon, memorandum 28/5/1888). But after the appearance of the disease in the mid 1890s, it was another matter. In the wild, diseased and distressed individuals were easily killed. When snared, diseased thylacines tended to stay snared, frequently made little attempt to free themselves, and often these infected individuals died as a result of the additional trauma of capture (Paddle, 2000).

Table 2. Total number of thylacines killed (adults and young) for each year of the government bounty scheme (n = 2,209).

Year	Adults killed	Young killed	Kill Total
1888 (May – Dec)	58	8	66
1889	110	4	114
1890	129	2	131
1891	89	3	92
1892	107	7	114
1893	104	8	112
1894	101	5	106
1895	104	5	109
1896	122	2	124
1897	106	10	116
1898	106	5	111
1899	122	11	133
1900	138	15	153
1901	157	11	168
1902	112	18	130
1903	85	3	88
1904	93	17	110
1905	101	15	116
1906	42	1	46
1907	47	4	49
1908	15	2	17
1909 (Jan – June)	2	0	2
Bounty Totals	2,050	159	2,209

To the background extermination rate being applied to thylacines because of its pest status, one has to add-in the effects of the disease. The disease increased the ease of capture, increased the likelihood of encountering dead thylacines in the bush, both snared and unsnared, and thus materially contributed to the number of bounty "kills" made. This may be read in both the government bounty and Woolnorth data, and suggests that the disease should enter the foreground in a consideration of the factors leading to the species' extinction.

Age-related effects of the disease are also suggested in the bounty data. Of the 159 juvenile thylacines identifiably procured for the government bounty between 1888 and 1909, a little over two-thirds (107) were presented for payment in just the first ten years of the initial spread of the disease, from 1896 to 1905 (Table 3). For this contingency table $\chi^2 = 7.8751$, $p < 0.01$, suggesting that, in the wild, juveniles were more susceptible to the disease than adults.

Table 3. Age separation of raw bounty data, for the first recognised decade of the disease, versus the other (eleven plus) bounty years.

	First Disease Decade (1896 – 1905)	Other Bounty Years (1888 – 1895, 1906 – 1909)
Adults	1,142	908
Juveniles	107	52

The maximum government pay-out in any one year was for 168 thylacines in 1901, representing a bounty paid, on average, close to once every two days. Such disease-assisted capture of Tasmania's dominant indigenous predator represented an unsustainable rate of kill likely to lead to the rapid extinction of the species. Just eight years later, when the bounty was finally terminated in 1909, the government was paying a bounty on a thylacine, on average, once every five months. Extinction duly followed.[4]

The Symptoms of the Disease in Captivity

The first appearance of the disease in zoological gardens around the turn of the twentieth century, was devastating in terms of marsupi-carnivore mortality. While not all thylacines (or Tasmanian devils for that matter) died at first contact, the episodic nature of the disease eventually wore them down, and long-term survivors were rare.

Melbourne Zoo

At the beginning of August 1900, Melbourne Zoo had six thylacines on display, an adult male and female pair and their four cubs (specimens *xvi* to *xxi*), the product of the only successful breeding of the species in captivity (Paddle, 2000). The vector or specimen that introduced the disease to Melbourne is unknown. Prime candidates, however, would be the three Tasmanian devils arriving at the zoo on 16th June 1900. When the disease surfaced and struck home, the thylacines went down like flies. As fast as they died, Melbourne replaced them, such that in the next 20 months 13 additional thylacine specimens (*xxii*, *xxiia*, and *xxiii* to *xxxiii*) were added to the display. Of these 19 specimens present or purchased between August 1900 and March 1902, all but one had died from the disease by 1st December 1902.

Initially, lesions on the skin were interpreted as instances of intraspecific aggression. One of the cubs bred in captivity (*xviii*) died on 19th August 1900, and was recorded as "Eaten by others". When one of the parents died on 24th May 1901, its bloody, damaged skin prompted the comment "Apparently killed by its mate" (Royal Melbourne Zoo, 1931a).

Thylacines appeared remarkably placid in captivity in the mixed social groupings in which they usually found themselves. Only two instances of intraspecific aggression were ever observed and recorded in the history of the zoological garden display of thylacines. In July 1889 one of two male thylacines, the sole occupants of a cage at Launceston City Park Zoo, attacked, killed and ate "a considerable portion" of the other (Trot, 1889). At Washington Zoo, late in the morning of 6th October 1905, a fight, unrelated to any feeding issue, broke out between an unrelated and isolated pair of thylacines, some nine weeks after they were first introduced to each other. The male had, the previous year, been successfully housed, without expressing aggressive intent, in an isolated pair with a mature, previously pair-bonded and mated-in-the-wild female (not unsurprisingly, this pairing was without issue). The new female was one of her offspring, an immature, virgin, three-year-old cub, who had "half of one ear bitten off & a bad cut on her head" (Blackburne, 7/10/1905). After immediate separation, the pair was later reunited, and spent a further 48 months living together as an isolated couple before the death of the male, without further recorded aggressive interaction, but also without breeding.

The post-mortem comments from Melbourne Zoo, above, on the first two deaths, unrelated to any recorded intraspecific aggression in the daily record book (Royal Melbourne Zoo, 1915), were made in the absence of any knowledge of the existence of a disease. Certainly, a thylacine body exhibiting significant hair loss and bloody skin lesions presents *prima facie* evidence of intraspecific aggression. But as the reality of the disease hit home, symptoms of infection becoming obvious in the specimens, and lesions and hair loss appearing on their bodies in the absence of any observed fighting, intraspecific aggression was ruled out of the equation. Some additional symptoms of dying thylacines are noted in the death book: *xxiv* (a female cub) "Died from Cold" (24/8/1901) – a comment indicative of infection, as distinct from the winterly "Died of cold" – and the juvenile male (*xxxii*) that died on 9th April 1902 exhibited "sore feet diarrhoea & weakness" (Royal Melbourne Zoo, 1931a).

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[4] The few thylacines surviving into the twentieth century, laid waste by human predation and disease, tended to show abnormal, stressed behaviour in their hunting practices, and frequently solitary existence. Oral history records on the behaviour of the species obtained from trappers and old-timers with personal knowledge of the thylacine in the twentieth century, reflect the reality of thylacine existence at the time, but tend to be atypical. Nineteenth-century records of the species – from both Indigenous and invasive European perspectives – identify the thylacine's typical social and hunting behaviours as based around a small, family group (as summarised in the second paragraph of the Introduction).

So rapid and constant proved the deaths, that causes and symptoms went unremarked in the death book, to the point where eventually the deaths themselves were recorded only spasmodically. For example, records from the National Museum of Victoria identify four different dates in July and August 1901 on which dead thylacines were received from Melbourne Zoo (National Museum of Victoria, 1903, 1915, 1923), but only one of these departures is recorded in the zoo's death book (Royal Melbourne Zoo, 1931a). Furthermore, the bodies of two of these four thylacines were in such poor condition that no attempt was made by museum staff to save the specimens. No date of death has been recorded for the single surviving specimen alive on 1st December 1902. Later that month another thylacine (*xxxiv*) was obtained from northern Tasmania, and this specimen, either because it was now the sole representative, or because it was judged to be the better in physical condition, was sent to Antwerp Zoological Gardens in January 1903. Unfortunately, though not surprisingly, it appears to have died on board ship before arrival. While the disease in Tasmania contributed to the ease of bounty claiming, it made trade in live thylacines a much more difficult proposition. After the arrival of the December 1902 specimen it was 18 months before Melbourne was again able to obtain another thylacine.

For the record, like the thylacine, Tasmanian devil deaths in Melbourne Zoo around this time were initially ascribed to intraspecific aggression (3/5/1899) – and devils being devils this may well have been the case in some instances – but certainly for later deaths, after the devil arrivals in June 1900, the problem was recognized as disease, described as "mange" (4/3/1902: Royal Melbourne Zoo, 1931a). Similar explanations of skin lesions as traumatic wounds, rather than dermatopathies, are recorded for Dasyurids at this time at London Zoo. Up to 1932, Dasyurid skin lesions were most frequently designated in London as "killed by companions" (Canfield & Cunningham, 1993, p163). Such explanatory bias, as these authors point out, "may have been identified, with histologic examination, as infectious or neoplastic in origin" (p164).

Before leaving Melbourne Zoo, having addressed the effects of the disease on its thylacines, a few reflections on the effects of the disease in the other marsupi-carnivores on display are offered. The precision in recording details of the smaller carnivores at Melbourne Zoo frequently lacks the specificity (and resulting individuation) accorded the larger carnivores. Certainly, some of the smaller marsupi-carnivores originated from Tasmania, others from Victoria and the other mainland states, but for many the original locality is unknown. For comparative purposes, native cat, or eastern quolls, *Dayurus viverrinus,* and tiger cats, or spotted-tailed quolls, *D. maculatus*, are known to live up to three years in the wild and, with the improved knowledge and care available in modern-day institutions, up to six years in captivity. For Tasmanian devils – pre the arrival of the facial tumour disease – life expectancy was up to six years in the wild, and eight years in captivity (Holz, 2008). To two existing nineteenth-century native cats, Melbourne added three further specimens between 1st June 1900 and 28th June 1901. All five died between 26th March 1900 and 1st September 1901. To the one tiger cat already on display, Melbourne added six more specimens between 20th December 1901 and 12th September 1902. Six of these died in the twelve months between 28th August 1902 and 26th August 1903. The seventh survived and respectably lived on in captivity until 23rd February 1905. To one existing nineteenth-century devil, Melbourne obtained nine additional specimens between 16th June 1900 and 28th October 1903. Five of these were used in specimen exchange with other zoological gardens. The five remaining incumbents had all died by 5th January 1904, with the disease confirmed in the *Death Book* (Royal Melbourne Zoo, 1931a) as being present in the devil display. Melbourne was unable to obtain any further devils for the next two-and-a-half years, but then they became readily available once again, most, however, not being in the peak of physical condition. In similar fashion to the earlier treatment of the thylacine display, Melbourne continuously replaced the devils as deaths occurred in the collection. In a little over a year, between 6th May 1907 and 25th July 1908, Melbourne obtained eleven devil specimens, two of which were successfully sent to the Zoological Society of London, but the other nine all died between 17th October 1907 and 2nd May 1909. The problem continued, but at a reduced level of morbidity. Some devils began to survive repeated contact with the disease and live to respectable ages in captivity, while others continued to succumb to its effects. The annual report on autopsies of Melbourne Zoo specimens carried out by the Veterinary School of the University of Melbourne, identified the cause of death of a devil that died in 1911, as due to the "no. lesions". The only other Dasyurid autopsied, an eastern native cat, died of the multifariously-origined "trauma", together with an "impacted rectum" (Stapley, letter 4/3/1912).[5]

Launceston Zoo

Wm. McGowan took over as Superintendent of Launceston City Park Zoo in June 1882, and obtained his first thylacines for display in 1885. Remarkably, the first occasion in the history of the zoo where expenditure was granted for the purchase of stock was not until 1921, when Launceston City Council approved the expenditure of £24/9/10 on the "Purchase of Birds" (City of Launceston, 1921). Up to then McGowan developed the zoo on the basis of donations and local exchanges with Tasmanian animal collectors; offering, for example, Australian mainland birds in exchange for thylacines (M. Turner, interview 25/10/1992) until, after the sale of specimens to mainland zoos, he was able to build up a small cash reserve for the purchase of exotic animals for Launceston. Fiscal requirements eventually forced McGowan to start negotiations over the sale or exchange of all his thylacines with other zoos. The presence of the epidemic disease saw him advertise widely for thylacine specimens (*Hobart*

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[5] Melbourne's only thylacine living in 1911, an adult of unknown sex (*xxxvii*), died in December 1913. The cause of death was not recorded, but the body was sent to the Veterinary School of the University of Melbourne, for post-mortem analysis and dissection. Unfortunately, no record of the post-mortem has been preserved in the archives of either institution.

Mercury, 16/7/1908, 18/7/1908), and necessarily obtain them from further afield than the depleted population in north-eastern Tasmania. It also encouraged him to speed up the process of sale and exchange. Between June 1901 and February 1906 McGowan obtained 24 thylacine specimens (*xxvi* to *xl*, *xla*, *xli* to *xlviii*), 16 of which he rapidly dispatched to Melbourne, Sydney (Moore Park) and Washington Zoos. Seven thylacines, however, died within days of their arrival in Launceston Zoo, before any sale or exchange could be effected.

Adelaide Zoo

Adelaide Zoo's thylacine display had temporarily ceased at the end of 1896, with the death of specimen *xiii* that had been on exhibit since August 1892. Adelaide managed to obtain nine thylacine specimens between January 1897 and September 1902, including an adult male (*xvii*) from Launceston Zoo on 15th June 1898 (Royal Zoological Society of South Australia, 1929). Shortly after this specimen arrived the thylacine display began to wind itself down. Two specimens died between July and November 1898, and two more in January and February 1899 (Hale, 1956). Two thylacines died at unspecified times in 1900. Two more deaths occurred in 1901, in July and September (South Australian Museum, 1907), and the last thylacine exhibited in Adelaide (*xxii*) died on 13th September 1902. No veterinary records or post-mortem comments have been preserved in the zoo archives for these nine specimens. The zoo destroyed the skin and post-cranial skeletons of two of these specimens, and not even the skull was preserved from a third death. Six specimens were considered at the zoo to be probably in good-enough condition to be donated to the South Australian Museum, and it is possible to specifically identify five of these in the Museum's current collection. While the skeletal material was preserved from all five specimens, only one of the skins was deemed worthy of preservation by museum staff. The loss of the last nine thylacines on display, between July 1898 and September 1902 matches the record of the epidemic disease on the ground in Tasmania, and that being experienced in Melbourne and Launceston Zoos. The known preservation of only one skin from these last nine specimens is most unusual, and strongly suggestive of their presentation with significant pelagic damage (*sensu* Dumpty, cited in Carroll, 1872).

New York Zoo

Despite the virulence of the disease at its first appearance, the occasional adult thylacine survived repeated bouts of the disease and lived into old age.

New York's first thylacine, "a fine male specimen" (Hornaday, 1903, p59) arrived at the Zoo on 17th December 1902, courtesy of Carl Hagenbeck, the Hamburg animal dealer. Despite its arrival in good condition, it was noted on 29th December that the thylacine was ill: "Tasmanian Wolf acts weak & indisposed. Took some chicken & milk" (Ditmars, 29/12/1902). The invalid food was apparently a success, as it was noted on the following day that the "Tasmanian Wolf fed well today" (Ditmars, 30/12/1902). This, the first of three bouts of illness, passed relatively quickly and without amplified comment.

The thylacine became ill again for the second time on 2nd February 1903 when, under "Illness worthy of note" in the mammal department's "Daily Report of Occurrences" it was noted, in similar fashion to the Melbourne Zoo records, that the "Tasmanian wolf has very sore feet" (Ditmars, 2/2/1903). This difficulty and pain in movement was again referred to the next day. The following day all was apparently well with the thylacine, and it was noted that, apart from a lemur which had died and an ocelot killed by some pumas, that "Everything else in good shape" (Ditmars, 4/2/1903). Once again, the illness passed fairly rapidly.

The next three and a half months passed uneventfully, but then the thylacine became ill for the third time. On 22nd May it was recorded: "Tasmanian Wolf very lame. Fed well last night, taking a pan of milk & all his meat" (Ditmars, 22/5/1903). The problem continued: "Tasmanian wolf very lame" (Ditmars, 23/5/1903); and the extent of the problem was mentioned the next day: "Tasmanian wolf has very sore feet. Den covered with blood" (Ditmars, 24/5/1903). Fortunately on the 25th it was noted "Tasmanian Wolf began feeding tonight. Took a young chicken" (Ditmars, 25/5/1903) and two days later it was recorded in the mammal department that the "General condition of the animals very good" (Ditmars, 27/5/1903). After three bouts of this disease, each increasing in magnitude, the thylacine never experienced the problem again, and survived in apparently healthy condition until 15th August 1908, when it was recorded "Tasmanian Wolf sick", and two days later, on 17th August "Tasmanian Wolf died" (Blair, 15/8/1908, 17/8/1908).

Beaumaris Zoo

For the first fifteen years after the disease became apparent in north-eastern Tasmanian marsupi-carnivores in the mid 1890s, it appeared particularly virulent and thylacines particularly vulnerable. During the next fifteen years, specimens killed or captured in the wild often exhibited skin lesions, and the trauma of capture, or the addition of being sent to a zoo, could still lead to death. Nevertheless, captive specimens now more frequently emulated the behaviour of the 1902 New York male, in that they would exhibit symptoms of the disease for a time, but would then recover. The presence of the disease in Mary Roberts' Beaumaris Zoo, Hobart, is offered as indicative of these times.[6]

A female thylacine purchased by Roberts was dead on its arrival at the zoo on 6th June 1911, and one of the two devils that accompanied it died the following day. The thylacine's body was kept at the Zoo for some little time, while Roberts enquired whether Prof T.T. Flynn at the University of Tasmania, was interested in preserving its internal organs. Among the marsupi-carnivores then on display in the zoo, to serve as potential carriers for the vector of the disease, were at least six Tasmanian devils and an adult female thylacine (*iii*) and her male cub (*vi*), both captured at Woolnorth in 1909.

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[6] In this paper, the name "Beaumaris Zoo" has been reserved for just the privately run Beaumaris Zoological Garden, established by Mary Roberts at Sandy Bay, on the then outskirts of Hobart, with its orientation towards the display of Tasmanian and Australian species. After Roberts' death in 1921, her collection formed the basis of the short-lived (1922 – 1937) Hobart City Council's zoological garden at the Domain, which officially preserved the name Beaumaris in its title, but now with a changed orientation towards the display of exotic species. This second iteration of Beaumaris Zoo is designated herein as "Hobart Zoo".

A large, adult male in fine condition (*viii*), with an unblemished skin, then arrived at the Zoo from Tyenna on 12th August 1911 (Paddle, 2008). Later in the month, this adult male developed a lesion on his tail. Concerned about his symptoms the veterinarian was called for: "Mr Ritchie Veterinary surgeon came to see the spot on tigers tail, sent powders and medicine" (Roberts, diary 25/8/1911). The male recovered, but the adult female then fell ill some weeks later. No specific symptoms were recorded on this occasion, merely a note that "Had the Veterinary Surgeon to see the female tiger in the morning, he thought she had a severe cold" (diary 11/9/1911). She also recovered, and did not trouble the veterinarian again. Her specific date of death is unrecorded, falling in a brief hiatus in Roberts' record-keeping, but appears to have taken place around March 1913. The adult male died on 9th March 1915. Writing later about the demise of the Woolnorth female and Tyenna male Roberts noted: "The pair were both old & died from that cause eventually" (Roberts, letter 27/3/1919).

The remaining young Beaumaris male (*vi*), whilst he remained in Roberts' care, showed no sign of the disease prior to his departure for London Zoo on 28th September 1911, just 17 days after his mother required veterinary attention. He arrived in London (as specimen *xix*) on 21st November 1911, but did not join the other thylacines on display, one of which was his male sibling. He was placed in the Zoo's sanatorium and remained there for over seven weeks (a suspiciously long quarantine time), during which time his sale to New York Zoo was negotiated. He left London Zoo on 10th January, and arrived at New York Zoo (as specimen *ii*) on 26th January 1912. Hornaday wrote to Roberts (letter 6/4/1912): "We have at last secured a fine Tasmanian Tiger, which is living in our Small-Mammal House, in good condition, and seems to be enjoying life". But despite this promising start, after only ten months of American display, he died on 20th November 1912. Unfortunately, the daily reports for the mammal department and veterinarian's office for 1912 have not been preserved in the New York Zoo archives. The only comment about its departure was that "while it arrived in good health, it was so nervous and unreconciled to captivity that it lived only a few months" (Hornaday, 1912, p71). This comment is rather anomalous, as the specimen had certainly proved well-adjusted to captivity in Hobart, having been caught, along with its mother and two of its siblings, as a young cub, around ten months of age, between late May and early June 1909. It died at a relatively young age, after a suspiciously short and troublesome period of display in New York, some 17 months after first-known contact with the disease.

Whilst on the topic of Beaumaris Zoo, a few observations on the marsupi-carnivore disease in Mary Roberts' devils are offered. Mary was certainly enamoured with her devils, became the first person to breed them in captivity (Roberts, 1915), and, all told, between April 1908 and August 1920 kept at least 82 specimens in captivity.[7]

There is no mention or indication of disease amongst the first 21 *Sarcophilus* specimens displayed in the zoo, between April 1908 and April 1911. The dates of death, or last reference to continued existence within a collection are known for sixteen of these specimens. None of these sixteen survived for less than five months in captivity, and one of the pouch young obtained in October 1908 (*Sviii*) died in Melbourne Zoo in March 1914, after 65 months of captive existence. Then three consecutive devils (*Sxxii* to *Sxxiv*), obtained by Roberts between 15/5/1911 and 6/6/1911, from three different localities (Triabunna, Little Swanport and the Lakes District) were all dead within 24 hours of their arrival. For the first time, in 1911, Mary began to refuse the offer of devils specimens, particularly those from Triabunna – even refusing the tempting offer of a mother with pouch young caught by E.E. Ford (Roberts, diary 28/8/1911, 29/8/1911). Until 1912 Mary paid the devil trappers on the day, if they arrived with their catch in person, or within one or two days of an unaccompanied devil's arrival, via postal note. But in 1912 she began to delay immediate payment for devil specimens, sometimes for more than three months (in the case of specimens *Sxli* and *Sxlii*), if she found them diseased on arrival (Roberts, diary 26/9/1912, account book 30/12/1912); and after April 1912 she refused to purchase any further devil specimens on offer from the trappers Ford and Harry Smith of Triabunna.

London Zoo

For the record, the three thylacines housed nearby to the quarantined Beaumaris specimen in London Zoo showed no obvious external sign of the disease on their bodies. One of them became ill, and was daily recorded as "unwell" between 30th January and 18th March 1913 (Zoological Society of London, 1913), but it recovered fully and lived for at least a further 15 months. All three London thylacines, however, died in 1914. The first (*xvi*) on 5th June from "Chronic Nephritis", another (*xvii*) on 20th November from "Peritonitis", and the last (*xviii*) on 25th December, also from "peritonitis", as a result of "perforation of colon" (Zoological Society of London, 1916). Of the eleven thylacines that died in London Zoo between 1884 and 1931, peritonitis was the identified cause in five cases, enteritis and nephritis accounted for two further deaths, and four departed without exciting post-mortem comment. Peritonitis, due to gastric ulceration, is a common marsupial stress-related condition as a response to prevailing captive conditions (Canfield & Cunningham, 1993). Similarly, nephritis was a common necroscopic diagnosis across all marsupial groups displayed in London Zoo (Canfield & Cunningham, 1993; Crisp, 1860; Plimmer, 1915). The female thylacine that died on 5th June 1914 of "Chronic Nephritis" is of greater interest here, howsoever, given the later veterinary analysis of nephritis accompanying deaths specifically ascribed to the epidemic disease in thylacines at Hobart Zoo.

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[7] The total of 82 displayed is a minimum estimate, and makes the assumption that all four devils that escaped during the night of 7/5/1911 were recaptured, and later sold or exchanged. It is unusual, however, that such hypothesized success in recovery failed to be recorded in Roberts' diary.

The marsupi-carnivore disease, however, certainly made inroads on London's devil collection. The specific life-histories are determinable for all five Tasmanian devils on display in London Zoo at the beginning of January 1911, prior to the unprecedented incidence of ante-mortem comment found in the *Daily Occurrence Records* (Zoological Society of London, 1911a, 1912) that preceded their deaths from the disease. The oldest, specimens *Sxv* and *Sxvi*, were both males that had arrived from Melbourne Zoo in June 1908. Specimen *Sxix*, of unrecorded sex, arrived from Beaumaris Zoo, also in June 1908 (together with two companions sold/exchanged to other institutions). The last two specimens, *Sxx* and *Sxxi*, of unrecorded sex, arrived from Beaumaris Zoo in November 1908. The source of infection for London's devils is unknown. The disease was not recorded at Beaumaris Zoo until May 1911, well after the despatch to London of all of specimens *Sxvii* to *Sxxi*. While the epidemic disease had appeared in the marsupi-carnivores at Melbourne Zoo in 1900, the devils received in London from Melbourne (*Sxv* and *Sxvi*) showed no sign of the disease for the relatively long period of time between June 1908 and January 1911.

One Tasmanian devil was recorded as "unwell" from 24th to 26th January 1911. Two Tasmanian devils were recorded as "unwell" from 28th to 31st January. One of these devils (*Sxv*) died on 1st February. The second devil remained "unwell" on the 1st and 2nd February, joined by a third "unwell" devil from 3rd to 5th February, with a fourth devil also recorded as "unwell" from 6th to 7th February. On 8th February *Sxx* died and was autopsied. As in previous zoological garden records for the first incidence of the disease, the lesions associated with the disease were described as "Injury, suppuration of wound" together with "gastric ulceration, tapeworms" (Zoological Society of London, 1911b). Specimens *Sxvi* and *Sxix* recovered, but *Sxxi* remained "unwell" on 8th and 9th February, before dying on 10th February. Post-mortem comment again interpreted the lesions as "Injury", together with "dilated heart, nutmeg liver, congestion of lungs" (Zoological Society of London, 1911b). On the same day, one of the two remaining devils was recorded as "unwell", and remained so until 14th February. Both devils were then recorded as "unwell" from 16th to 19th February, but one of these recovered. A devil was recorded as "unwell" on a daily basis for the next 53 days, between 20th February to 13th April, then both appeared healthy and failed to trouble the daily records for some little time. Four months passed before the disease returned again. One devil was recorded as "unwell" from 26 August 1911 to 29th September, both appeared healthy on 30th September, then the other devil became "unwell" from 1st to 19th October. Both successfully survived this second bout of disease, but they succumbed when it returned for the third time two months later. *Sxvi* died on 2nd January, and *Sxix* died on 23rd January 1912. Neither of these specimens was autopsied.

Hobart Zoo

No zoological garden proved able to obtain thylacine specimens directly from the wild in 1926 or 1927. At Hobart Zoo, under the curatorship of Arthur Reid (and later his daughter Alison), come the end of 1927, two female thylacines remained on display. But, for a brief time in 1928, thylacine availability changed, for the worst of all possible reasons, as a particularly virulent strain of the disease appeared in the species once again, and distressed thylacines appear to have become more readily encountered and captured in the bush. To the two already in stock, a further seven specimens (*xx* to *xxvi*) were added in the first four months of 1928. By the end of the year, however, only two of these nine specimens remained alive. While such virulence hardly represents effective use of a host species by a disease organism, it is readily explicable, given that the disease does not appear to have been restricted to a single host species (de Castro & Bolker, 2005; McCallum & Dobson, 1995).

Arthur Reid considered that the disease was "perhaps distemper that they had caught from the trapper's dogs", but Alison Reid was less convinced: "there wasn't any sign of discharge from the eyes and nose like you see with a [distempered] dog … they just died" (Alison Reid, interview 1980). While it is now known that canine distemper virus can spillover to non-canid species (Roelke-Parker, *et al.* 1996), against the direct spillover of distemper between the two species is a contemporary suggestion that it was only after the wild dogs in the bush had died of distemper that thylacines became common (*Tasmanian Mail*, 9/8/1884).

An adult female with two pouch young (*xx* to *xxii*) entered the zoo on 10th January 1928. A product of the previous peak breeding season in early spring, the cubs "were fairly advanced, they were just about on the point of emerging when they came in" (Alison Reid, interview 27/2/1992). The new arrivals joined the two resident females in the thylacine cage on the hill at the back of the zoo.

A fortnight later, on 24th January another thylacine (*xxiii*), a juvenile male arrived at the zoo, brought in some haste by its captor, T. Hunt of Tyenna. Obviously ill on its arrival - "There was one very sick one that came in with a virus, it came from Tyenna" (Alison Reid, interview 20/10/1995) - it was not added to the collected thylacine display, but caged alone near the front entrance of the zoo. The photographer Ben Shepherd, of Sandy Bay, visited the zoo within days of its arrival and took a glass half-plate negative of the diseased specimen (Figure 1). Shepherd provided the scientific illustrator and photographer, Norman Laird, with a copy from the negative, and details of the specimen and its photography. As recorded in an unpublished manuscript by Laird: "The animal died the day after it was photographed, and it does not represent the species in good condition" (Laird, ca1978). Despite the relative isolation of its display, alone in its cage at the front of the zoo, "that was where the sick one came but the virus seemed to spread right up to the other [cage]" (Alison Reid, interview 20/10/1995).

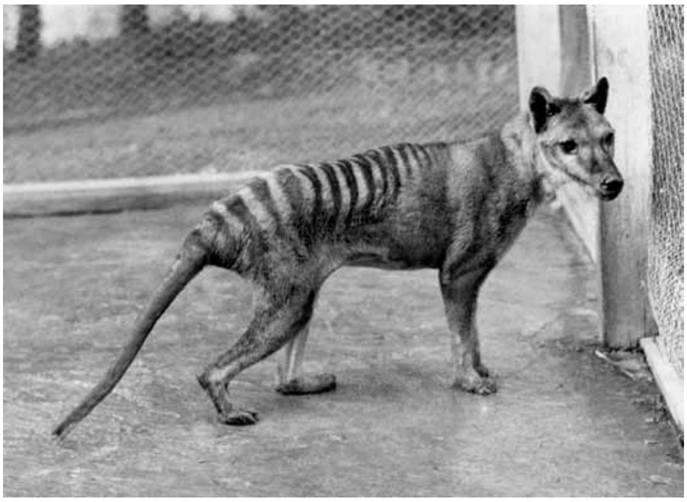

Figure 1. The diseased Tyenna male (*xxiii*), caged separately in Hobart Zoo, late January/early February 1928, on the penultimate day of its existence. (Shepherd)

This juvenile Tyenna male died at the end of January, or very early into February 1928. No further thylacine deaths were recorded in the monthly stock mortality list from 14th February to 13th March. In fact, an additional juvenile female thylacine (*xxiv*) had arrived on 28th February. It was not until two months after the young Tyenna male had arrived (and rapidly departed), that the animals displayed in the thylacine cage proper, up the hill at the back of the zoo, started dying. As Alison Reid recalled:

- they just sort of keeled over and died. (interview 27/2/1992)
- We were pretty badly hit, because all of ours died, one after the other, they all died. (interview 24/6/1996)

The first to die, on 20th March 1928, was one of the newly arrived cubs, a female (*xxi*). Its skin was in good condition, and the cub was sold to the Tasmanian Museum, where it was mounted by Alison Reid. Then, on 27th March Arthur Reid reported to the Reserves Committee meeting that "one of the female Tasmanian Wolves had died", not the 10th January mother, but one of the two females on hand at the start of the year. The skin of this specimen was in poor condition. Although externally unsuitable for public display, her body was sold for internal display to Colin MacKenzie of the Museum of Comparative Anatomy, Melbourne (the collection later moving interstate to become the Institute of Anatomy, Canberra).

With three thylacines lost already this year, and with their value as exchange or sale specimens appreciating, the Reserves Committee promptly sent Arthur Reid to Port Davey, as he "had been informed there was a number of Tasmanian Wolves there" (Reserves Committee minutes, 27/3/1928). The visit was successful, Arthur Reid returning with a pair of thylacines (*xxvi* and *xxvii*) on 17th April 1928.

From April 1928 onwards, thylacine deaths ceased to be significant events, becoming almost matter-of-fact occurrences, Arthur just "used to say 'another tiger died'" (Alison Reid, interview 27/2/1992). Because of the poor quality of the skins, possessing significant areas of active lesions and hair loss; the bodies of three out of the next four thylacines to die were not offered as museum specimens. Daily, rather than weekly, rubbish collection from the zoo only commenced in 1931 (Reserves Committee, minutes 20/7/1931), and, as dead thylacine bodies were a bit too large to hang around for up to a week, the corpses were buried "in the zoo, up on the bank" (Alison Reid, interview 25/6/1992). The only specimen whose body was deemed worthy of preservation was that of a juvenile female that died on 18th July 1928, was purchased by the Tasmanian Museum and duly preserved as a mounted display.

Two thylacines survived the year, although continuing at times to show periodic evidence of the disease. They were both on display when Arthur Reid drew up the "statement of stock" on 31st October 1929, but one of them died the next day: "The Curator … reported that one Tasmanian Wolf had died of kidney disease" (Reserves Committee, minutes 1/11/1929). The body was sold to MacKenzie for anatomical purposes. The designation of "kidney disease" is interesting, and has parallels with the thylacine death at London Zoo on 5th June 1914. Alison Reid was persistent (interview 24/6/1996) in her opinion that all thylacines present in 1928 eventually died of the epidemic disease. The veterinary surgeon, Dr C.M. Sprent visited the zoo twice, in early October and again in late October or early November 1929 to examine the thylacines (Alison Reid, interview 1980; Reserves Committee, minutes 14/10/1929, 18/11/1929), and is the likely source for the inference of renal failure.

The last of the zoo's thylacines present in 1928 died of the disease five months later, missing from the stock report of 31st March 1930. "The Curator reported that the Tasmanian Wolf had died of kidney disease" (Reserves Committee minutes, 14/4/1930). Presumably the identification, once again, of death from "kidney disease" was a diagnosis of the veterinary surgeon's, but it is not known whether Sprent was called to the zoo at the time of the thylacine's death, for the record of accounts paid between 18th and 30th March 1930 are missing from the zoo archives. It was seven months before the zoo was able to obtain another thylacine for display.

It is not known for certain whether the Hobart Zoo loss of all nine thylacines to disease, between January 1928 and March 1930, was paralleled elsewhere. James Harrison, estate agent and animal dealer in Wynyard, recorded the purchase of two live thylacines from an unidentified source around April 1928: a juvenile for £7/10/- and an adult for £20. Both were sold to Colin MacKenzie in May 1928. The juvenile had died in Harrison's care, and its body was sold to MacKenzie for just £12, but Harrison demanded and received £50 for the live adult (Harrison, 1931) which was immediately deposited in Melbourne Zoo. Melbourne had two thylacines on display in 1927, and obtained just two more specimens from the wild, on 11th May 1928 and 16th October 1929. Unfortunately, due to the loss of archival records from the Zoo, as well as the Institute of Anatomy (the repository of the bodies of the last six Melbourne Zoo thylacines on display), the death date of only one of these last four Melbourne specimens is known, that of the last thylacine received,

Table 4. The number of thylacines, and time span of their display (from the arrival date of the first specimen, to the departure date of the last), in public access zoological gardens, by locality and initial date of display. Uncertainty over the terminal display marked with "?".

Locality	Years Displayed	No. Thylacines	Locality	Years Displayed	No. Thylacines
Tasmanian			**International**		
Propsting, Hobart	1854 – 1856(?)	1	London	1850 – 1931	20
Launceston	1885 – 1925	66	Berlin	1864 – 1908	4
Roberts, Hobart	1909 – 1921	16	Paris	1886 – 1891	2
Hobart Council	1921 – 1936	29	Madras	1886 – (?)	2
Australian mainland			Liverpool	1888 – (?)	1
Melbourne	1864 – 1932(?)	48	Washington	1902 – 1909	5
Adelaide	1885 – 1902	22	Cologne	1903 – 1910	2
Moore Park, Sydney	1885 – 1905	2	New York	1903 – 1909	4
Taronga, Sydney	1918 – 1923	1	Antwerp	1912 – 1914	1

whose death occurred on 18th July 1930. (For the record, the thylacine continues to be recorded in the stock lists accompanying the annual reports published in 1931 and 1932 [Royal Melbourne Zoo, 1931b, 1932], but these lists have proven to be a remarkably flawed data source, and inclusion therein is not, alone, indisputable proof that the species remained on display in Melbourne after July 1930.)

The Cumulative Effects of the Disease in Captivity

To date, research has identified 226 instances of the display of thylacines in public access zoological gardens (Table 4). This research is ongoing and continues to expand, largely as a result of the discovery of newspaper comments on thylacine display, which complement knowledge-gaps from incomplete archival holdings.

Longevity data is now available for 115 thylacines with a personal captive history, whose dates of death have been determined from zoological-garden and museum archives. The length of life in captivity is taken, either from the initial date of capture, where known, or from the date of arrival at the first zoological garden at which a specimen was displayed. None of these zoological gardens obtained thylacine specimens for the three years between 1894 and 1896. This hiatus close to the first acknowledged appearance of the disease in Tasmania (and realistically, not altogether unrelated to it) is used to separate the captive thylacine data; with zoological-garden arrival pre 1896 (Table 5) considered as being pre the likely presence of the disease in the locality of capture, and zoological-garden arrival post 1896 (Table 6) considered as being potentially post the likely appearance of the disease in the capture locality. The mean longevity in captivity for the pre disease cohort ($n = 32$) was 50.47 months ($sd = 32.20$), for the post disease cohort ($n = 83$) longevity was more than halved ($M = 23.24$ months, $sd = 27.71$); a reduction of 54%. Arguably, the strength of this data obviates the need for any statistical analysis, but for the record (and the pedantic) for a one-tailed test, $t = 4.1615$, and $p < 0.00007$.[8]

Estimates of specimen age at the commencement of captivity have been obtained from the archives for 111 of these 115 thylacines. The category of "Juvenile" used here encompasses zoological-garden description of newly arrived thylacines as "cubs", "young", 'juveniles", "three-quarters grown" and "near adult", or, in the absence of any descriptive label, a purchase price around 40 – 70% of that previously paid for known adult specimens. Age-related effects are powerfully present in this data (Table 7). Pre the appearance of the disease, the captive longevity of thylacines arriving as juveniles, as one would normally expect, exceeded the captive longevity of thylacines arriving as adults. But post 1896, this situation was reversed. While adult captive longevity was reduced by 43%, post the appearance of the disease, juvenile captive longevity was diminished by an impressive 69%. (One other factor, of relevance to the epidemic disease, may also be read from this table. The relative proportion of captive juveniles obtained, pre and post 1896, suggests at least that the disease organism did not significantly affect thylacine-host fecundity.)

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[8] Demanding a fixed date for departure deprives Table 6 of numerous post-disease captive thylacines lacking an identifiable personal history after their arrival and recorded date of death, but for whom an estimated maximum longevity could have been constructed and used in computation. For example, the only known details of two late-arrival thylacines at Hobart Zoo are their arrival dates: *xxvii*, an adult male which arrived in June 1930, and died sometime between that date and July 1931; and *xxviii*, a juvenile of unknown sex, which arrived in August 1931, and died sometime between that date and November 1931. The maximum captive longevity for both these specimens would be 13 months and three months respectively. Additionally, the date of death for seven of Melbourne Zoo's 19 thylacines held between August 1900 and March 1902 are unknown, but given the stock record of 1st December 1902, at a maximum, these seven could all have lived only until November 1902, thus the maximum captive longevity for these seven specimens would range between eight and 24 months. However, none of the above specimens, or thylacines with similar unrecorded personal histories and death dates, have their data included in Table 6. Their inclusion would have further lowered the determined mean longevity figure. It needs to be recognized that the decision to restrict the data in Table 6 to only include those thylacines with specific personal histories and departure dates limits the available data, and directly leads to an *overestimation* of the captive longevity achieved by thylacines post the appearance of the disease.

Table 5. Determinable longevity, measured in months, for zoological garden thylacines captured before 1896, prior to the first appearance of the disease.

Initial Zoo	Specimen Number	Capture/ Arrival Date	Arrival Age	Sex	Ultimate Zoo	Specimen Number	Death Date	Longevity (months)
ZSL	i	11/1849	jv	M			9/1853	46
ZSL	ii	5/1849	jv	F			5/1857	96
ZSL	iii	4/1856	ad	M	BRL	i	11/1864	103
ZSL	iv	1/1863	jv	M			4/1865	27
ZSL	v	1/1863	jv	F			1/1870	84
ZSL	vi	9/1884	ad	M			2/1890	65
ZSL	vii	9/1884	ad	F			4/1893	103
RMZ	i	11/1864	ad	M			1/1869	50
RMZ	ii	2/1874	ad	M			10/1881	92
RMZ	iii	4/1875	?	?			6/1875	2
RMZ	iv	4/1875	ad	F			12/1881	80
RMZ	v	8/1883	ad	M			1/1884	5
RMZ	vi	8/1883	ad	F			1/1884	5
RMZ	vii	1/1884	ad	M	PRS	i	3/1891	86
RMZ	viii	1/1884	ad	F	PRS	ii	2/1891	85
RMZ	xiii	6/1887	?	F			2/1892	56
BRL	ii	6/1871	ad	M			6/1873	24
LCP	i	6/1885	ad	?	ADL	i	9/1886	15
LCP	iii	11/1885	jv	F	ZSL	x	7/1888	32
LCP	v	6/1886	jv	M	ZSL	xiii	7/1894	97
LCP	vi	8/1886	ad	F	ZSL	xii	9/1891	61
LCP	x	1/1889	jv	?	ADL	viii	2/1891	25
LCP	xi	4/1889	jv	?	ADL	ix	2/1891	22
LCP	xii	7/1889	ad	M			7/1889	0
LCP	xiii	7/1889	ad	M	RMZ	xiv	4/1893	45
LCP	xiv	8/1889	ad	F	RMZ	xiva	10/1892	38
LCP	xv	8/1889	jv	?	RMZ	xv	6/1895	70
LCP	xvi	8/1889	jv	M	ADL	xii	5/1893	45
LCP	xvii	8/1889	jv	?	ADL	iii	4/1896	80
MPS	i	10/1885	?	?			2/1887	16
ADL	x	7/1890	ad	?			9/1892	26
ADL	xi	7/1890	ad	F			5/1893	34

Initial Zoo: ADL: Adelaide Zoo; ANT: Antwerp Zoo; BRL: Berlin Zoo; CLN: Cologne Zoo; HBZ: Hobart Zoo; LCP: Launceston City Park Zoo; MPS: Moore Park Zoo, Sydney; MRB: Mary Roberts' Beaumaris Zoo, Hobart; NYZ: New York Zoo; PRS: Jardin des Plantes, Paris; RMZ: Royal Melbourne Zoo; TZS: Taronga Park Zoo, Sydney; WSH: Washington Zoo; ZSL: Regent's Park Zoo, London.

Capture/Arrival Date: Earliest known record of the specimen in captivity (month/year). Capture dates, often established from non zoological-garden sources, may precede the official arrival date of a specimen at its initial zoological garden, by as much as six months.

Ultimate Zoo: Recorded only if specimen exchanged or on-sold. See abbreviations above. Note that other zoological garden display may intrude between the initial and ultimate locations.

Arrival Age: ad: Adult; jv: Juvenile, referring to specimens up to two years of age and three-quarters grown that, in the wild, would either still remain in the company of their parents, or have recently commenced a short-term solitary adolescent existence.

Table 6. Determinable longevity, measured in months, for zoological garden thylacines obtained after December 1896, post the first appearance of the disease.

Initial Zoo	Specimen Number	Capture/ Arrival Date	Arrival Age	Sex	Ultimate Zoo	Specimen Number	Death Date	Longevity (months)
ADL	xiv	8/1896	ad	M			9/1898	25
ADL	xv	1/1897	ad	F			9/1898	20
ADL	xvi	8/1897	ad	F			2/1900	30
ADL	xviii	11/1898	ad	F			7/1901	32
ADL	xix	11/1898	jv	M			1/1899	2

Initial Zoo	Specimen Number	Capture/ Arrival Date	Arrival Age	Sex	Ultimate Zoo	Specimen Number	Death Date	Longevity (months)
ADL	xx	11/1898	jv	M			2/1899	3
LCP	xxii	6/1898	ad	M	ADL	xvii	9/1901	39
LCP	xxiii	12/1898	ad	?	RMZ	xvi	5/1901	29
LCP	xxviii	6/1901	jv	F	RMZ	xxiv	8/1901	2
LCP	xxix	5/1901	ad	?			6/1901	1
LCP	xxx	7/1901	ad	?			8/1901	1
LCP	xxxii	11/1901	ad	?	RMZ	xxviii	12/1901	1
LCP	xxxv	4/1902	ad	F	WSH	i	11/1903	31
LCP	xxxvi	4/1902	jv	F	WSH	ii	9/1902	5
LCP	xxxvii	4/1902	jv	M	WSH	iii	1/1905	33
LCP	xxxviii	4/1902	jv	F	WSH	iv	10/1909	90
LCP	xxxix	8/1902	jv	?			8/1902	0
LCP	xli	4/1903	jv	?	MPS	ii	9/1905	29
LCP	xlii	4/1904	jv	M			5/1904	1
LCP	xliv	5/1904	ad	M	WSH	v	10/1909	65
LCP	xlv	8/1903	ad	F	RMZ	xxxvi	1/1905	17
LCP	xlvi	1/1906	ad	F			2/1906	1
LCP	xlvii	1/1906	jv	?			2/1906	1
LCP	xlviii	1/1906	jv	?			2/1906	1
LCP	xlix	9/1908	ad	M	MRB	ii	2/1909	5
LCP	l	9/1908	ad	F			11/1908	2
LCP	li	8/1911	jv	?			9/1911	1
LCP	lii	8/1911	jv	?			9/1911	1
LCP	liii	8/1913	ad	F			9/1913	1
LCP	liv	8/1913	jv				9/1913	1
LCP	lv	8/1913	jv	?			9/1913	1
LCP	lvi	8/1913	jv	?			9/1913	1
LCP	lvii	9/1915	jv	?			11/1915	2
LCP	lviii	9/1915	jv	?			11/1915	2
LCP	lix	11/1918	ad	F	MRB	xvi	3/1919	4
RMZ	xviii	9/1899	jv	?			8/1900	11
RMZ	xix	9/1899	jv	?			5/1901	20
RMZ	xx	9/1899	jv	F			7/1901	22
RMZ	xxi	9/1899	jv	M			7/1901	22
RMZ	xxiii	6/1901	jv	?			6/1901	0
RMZ	xxiv	6/1901	jv	F			8/1901	2
RMZ	xxix	12/1901	ad	?			12/1901	0
RMZ	xxx	12/1901	ad	F			5/1902	5
RMZ	xxxi	12/1901	ad	?			6/1902	6
RMZ	xxxii	3/1902	jv	M			4/1902	1
RMZ	xxxiv	12/1902	ad	?			2/1903	2
RMZ	xxxvii	9/1910	ad	?			12/1913	39
RMZ	xxxviii	12/1913	jv	?			6/1914	6
RMZ	xl	12/1913	jv	F			12/1921	96
RMZ	xli	5/1916	ad	M			12/1923	91
RMZ	xlii	10/1923	?	?			12/1923	2
RMZ	xlvi	6/1929	jv	?			7/1930	13
ZSL	xiv	3/1901	ad	M			2/1902	11

Initial Zoo	Specimen Number	Capture/ Arrival Date	Arrival Age	Sex	Ultimate Zoo	Specimen Number	Death Date	Longevity (months)
ZSL	xv	3/1902	jv	M			1/1906	46
BRL	iii	2/1902	ad	F			12/1905	46
BRL	iv	2/1902	ad	M			1/1908	71
CLN	i	3/1903	jv	M			9/1909	78
CLN	ii	5/1903	ad	M			5/1910	84
NYZ	i	10/1903	ad	M			8/1908	58
NYZ	iii	6/1916	ad	M			11/1916	5
MRB	i	10/1908	ad	F	ZSL	xvi	6/1914	68
MRB	iii	5/1909	ad	F			3/1913	46
MRB	iv	5/1909	jv	M	ZSL	xvii	11/1914	66
MRB	v	6/1909	jv	F	(ZSL)	d.o.a.	11/1910	17
MRB	vi	6/1909	jv	M	NYZ	ii	11/1912	41
MRB	vii	6/1910	jv	M	ZSL	xviii	12/1914	54
MRB	viii	8/1911	ad	M			3/1915	43
MRB	ix	5/1912	jv	?			5/1912	0
MRB	x	5/1912	jv	?			5/1912	0
MRB	xii	6/1916	ad	F	TZS	i	11/1923	89
MRB	xiii	6/1916	jv	M	NYZ	iv	9/1919	39
MRB	xiv	6/1917	ad	M	HBZ	i	10/1922	64
ANT	i	2/1912	jv	M			2/1914	24
HBZ	ii	6/1923	ad	?			6/1923	0
HBZ	iii	7/1923	ad	F			12/1923	5
HBZ	vi	2/1924	jv	?			4/1924	2
HBZ	vii	2/1924	jv	?			7/1925	17
HBZ	xi	8/1924	ad	F	ZSL	xx	8/1931	84
HBZ	xii	8/1924	jv	?			6/1925	10
HBZ	xviii	8/1925	ad	F			9/1925	1
HBZ	xxi	1/1928	jv	?			3/1928	2
HBZ	xxiii	1/1928	jv	M			2/1928	1
HBZ	xxix	6/1933	ad	F			9/1936	39

Categories as per Table 5.

Table 7. Mean thylacine longevity in months, (and standard deviations), by specimen age at time of initial capture, pre (<1896) and post (>1896) the appearance of the disease.

Longevity:	**<1896**	**>1896**
Adults	50.94 (33.81) n = 18	29.77 (29.12) n = 39
Juveniles	56.73 (27.94) n = 11	17.81 (25.19) n = 43

Summary of the Epidemic Disease Effects

The disease was episodic, recurring every two to four months (until full recovery or death), with no evidence of seasonal variation. As well as the thylacine, the disease also affected the Tasmanian devil, native cat and native tiger. Its initial appearance, at present, appears to have occurred in north-eastern Tasmania, around St Helens, in 1896. The disease reached the tip of north-western Tasmania, at Woolnorth, in 1901, the infection travelling a little over 200km in this six-year period.

The over-all effect of the disease in the wild, post 1896 was an increased rate of dead specimens presented for public and private bounties. In zoological gardens, between 1896 and 1936, adult captive longevity was reduced by 43%, juvenile captive longevity reduced by 69%, with no sex differences apparent in these captive mortality effects.

Professional verbal descriptors (from zoological garden curators) include: “Cold”, “distemper”, and “mange”. Professional autopsied comment (from zoological garden veterinarians) include the external appearance of “lesions”; and internal presence of “kidney disease”. The signs of the disease in captivity included coughing (as distinct from the “coughing bark” a social location and identification call of the species), refusal of food, and diarrhoea, eventually leading to “poor condition” and “weakness”. Prior to the last stages of the disease and death, distressed individuals showed normal levels of activity, with some difficulty of movement (“lameness”) occasionally noted – but whether this was typical of the disease (pain and stiffness in the lumbar region due to inflammation of the kidneys) or alternatively the response of infected individuals possessing actively-bleeding lesions particularly on the legs and feet ("den covered with blood") is unclear.

The initial expression of the disease in thylacines, from 1896 to 1910, saw massive, clumped, significant hair loss, with exposed skin consisting of deep-seated, actively-bleeding lesions. The depth of the problem was indicated by the difficulty in obtaining an intact skin for preservation from a diseased individual - areas of "rotten" skin made entire removal of the pelt difficult. There is little evidence for the formation of significant scabs, or a hardening and folding of the skin as in sarcoptic mange. Occasionally recovered individuals re-grew their hair over the former site of lesions in similar pattern to the hair originally lost. This was a period of high mortality.

The mid-period expression of the disease, from 1911 to 1925, saw it largely expressed as minor, spotted hair-loss, with bleeding active on the exposed skin, accompanied by reduced levels of mortality.

The late-period expression of the disease, from 1926 to 1936, saw at a minimum, poor coat and condition, with widespread, but not clumped, loss of hair, and no overt sign of bleeding, to, at a maximum, a return of the significant, large-scale hair loss and bleeding typical of its initial expression. There was also a return to the earlier high levels of mortality, that concluded with the extinction of the species.

Conclusion

Granted that the captive longevity and mortality data presented above may not be directly transferable to wild thylacine populations, nevertheless, changes in the wild behaviour of the species, represented by a growing ease of capture and killing, as recorded qualitatively in written and oral accounts from the wild, and quantitatively in the different bounty statistics, are supported by this additional qualitative and quantitative data from zoological gardens. The increased presentation of dead juvenile thylacines for government bounty payment after the disease first became apparent, and the rapid drop in bounty payment frequency from once every two days to once every five months, suggests that the longevity and mortality effects of the disease in the wild were not all that dissimilar to the effects recorded for the disease in captivity.

Captive data and bounty-capture records indicate, certainly in the first fifteen years of its recognised presence, 1896 to 1910, that the disease occurred with both high prevalence and high mortality in thylacines. Such characteristics are not unusual when a disease is not restricted to a single host species (McCallum & Dobson, 1995). For the disease occurred in other Tasmanian marsupi-carnivores, and likely contributed to the significant lack of genetic diversity in present-day devil populations in Tasmania (Siddle *et al.* 2010). It was also expressed on the Australian mainland (Lunney & Leary, 1988) – courtesy of migrating birds, bats or humans and their commensals - where, along with the introduced meso-predators of fox and feral cat (Johnson, 2006) it is likely to have been a significant factor in the extermination of the native cat from mainland Australia.[9]

The expression of this marsupi-carnivore disease in a variety of species, with a variety of outcomes – from extinction (of the largest species) to major extermination, and from population reduction to later recovery and expansion – demonstrates both the potential of disease to contribute to mammalian extinction, as well as the potential of an hyperdisease, across many species, to lead to multiple mammalian extinctions, as has been hypothesized for the late Pleistocene (Lyons *et al.* 2004; MacPhee & Marx, 1997).

In hindsight, without the disease, unquestionably a continuation of the unfettered habitat destruction, environmental degradation and the deliberate targeting of the thylacine as a pest, would have pushed the species to extinction. It just would have taken a significantly longer period of time, and the chance of saving the species, through changing public opinion, and the re-establishment of captive breeding, could have been possible. But the marsupi-carnivore disease, with its dramatic effect on individual thylacine longevity and juvenile mortality, came far too soon, and spread far too quickly. As such, this epidemic disease demands recognition, alongside habitat destruction, environmental degradation and deliberate killing, as the final causative straw that broke the thylacine's back.

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[9] This unusual biogeographic instance in the native cat, of continental extermination alongside insular recovery and survival, is also paralleled in the history of the rufous wallaby, *Thylogale billardierii*, whose sudden disappearance from mainland Australia at the turn of the twentieth century, may well be related to the existence of a macropod disease, certainly present and expressed within the Tasmanian population of the species. "About the year 1890 a disease broke out amongst the wallabies at Middlesex, which killed the animals in such numbers that it was thought they had been quite exterminated. All over the bush their dead bodies could be found, without any apparent traces of the disease. However, later on they slowly increased again in numbers, and became more numerous than before" (Weindorfer and Francis, 1920, p12). Once again, in this instance, it was not the continental but the insular population that recovered.

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